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Dioptrics of the facet lenses in the dorsal rim area of the cricket *Gryllus bimaculatus*

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Abstract 1. The optics of the corneal facet lenses from the dorsal rim area (DRA) and from the dorso-lateral areas (DA) of the compound eye of the cricket *Gryllus bimaculatus* were studied.
2. The DRA of the cricket eye contains quite normally shaped facet lenses. The diameter of the facet lens in the DA is 2-fold larger compared to that in the DRA. The radius of curvature of the front surface is distinctly less in the DA facet lenses, as the surface of the facet lenses in the DRA are virtually flat.
3. The averaged axial refractive index of the facet lenses of *Gryllus bimaculatus*, measured by interference microscopy, was 1.496 ± 0.008 ($n = 42$) in the DRA and 1.469 ± 0.004 ($n = 39$) in the DA. The geometrical thickness of the lenses was calculated to be 77 ± 3 μm ($n = 42$) in the DRA and 56 ± 1 μm ($n = 39$) in the DA.
4. Analysis of the diffraction pattern obtained with a point light source revealed distinct focusing properties of both the DRA and the DA facet lenses; striking Airy-like diffraction patterns were obtained in both cases.
5. Focal distances measured directly at the backfocal plane were 40 ± 8 μm ($n = 84$) in the DRA of all the animals studied, and 60–90 μm ($n = 62$) in DA depending on the animal. Analysis of the diffraction of the point light source yielded very similar focal distances: 40 ± 5 μm ($n = 10$) in DRA and 81 ± 8 μm ($n = 11$) in DA. In the DRA, focal distance of the facet lenses was smaller than the cone length, 58 ± 3 μm ($n = 9$) while in the DA the focal distance matched the effective cone length, 71 ± 5 μm ($n = 16$).

Key words Cricket · Facet lens · Dorsal rim area · Dioptrics

Abbreviations *DA* dorso-lateral area · *DRA* dorsal rim area

Introduction

The dorsal rim area (DRA) is a specialized part of the compound eye, well described in many species of insects (review: Labhart et al. 1992; Stavenga 1992; Labhart and Meyer 1993). The unique feature of the DRA is that it comprises photoreceptors of one spectral type with large polarization sensitivity (crickets: Labhart et al. 1984; Nilsson et al. 1987; Zufall et al. 1989; Gribakin and Ukhanov 1993b). Behavioral experiments proved unambiguously that E-vector orientation is mediated by these particular photoreceptors (crickets: Brunner and Labhart 1987; bees: Wehner and Strasser 1985; flies: von Philipsborn and Labhart 1990). Recently, we measured the polarization sensitivity of photoreceptors in the DRA of the cricket *Gryllus bimaculatus* and thus confirmed earlier findings of Labhart et al. (1984) that these photoreceptors can have an extremely high sensitivity to polarized light (up to 42; Gribakin and Ukhanov 1993b). The hypothesis that a very high polarization sensitivity can be caused by optical coupling seems to be unlikely, because stray light "floods this part of the eye" due to the complete lack of screening pigments (Burghause 1979; Nilsson et al. 1987).

Recently it has been assumed that light-scattering could be one of the reasons for high polarization sensitivity of the DRA photoreceptors in the cricket (Gribakin and Ukhanov 1993b). This assumption goes back to Waterman (1975), who presumed that

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a scattering polarizer underlies polarized light sensitivity in some animals. To investigate the possible existence of a strongly polarizing medium we have studied the geometrical optics as well as diffraction properties of the facet lenses of the DRA and of the adjacent dorso-lateral area part of the compound eye in the cricket *Gryllus bimaculatus*.

Materials and methods

Microreflectrometry

Live crickets, both adult males and females *Gryllus bimaculatus*, were mounted with wax and adhensive tape in a half-sphere holder. The animal then was adjusted so that the corneal surface of the DRA (Fig. 1a, arrows) or that of the adjacent dorso-lateral area (DA) was approximately orthogonal with an optical axis of a Zeiss photomicroscope, equipped with an epi-illuminator. The outer surface of the cornea in the DRA (Fig. 1b) is very smooth, because the facet lenses are virtually flat (Burghause 1979). The radius of curvature of the outer (front) surface of the facet lenses was determined following the procedure of Stavenga and Leertouwer (1990). In brief, an annulus pattern (Fig. 2a) was imaged by the lens surface (Fig. 2c, d). Considering the surface as a spherical mirror, one can calculate the radius of curvature, R, from the magnification, m, and the distance between object and image patterns, c, from $R = 2\ \mathrm{cm}/(1 - m^2)$. Similarly, the radius of curvature of both the outer and inner surface was determined on isolated corneas immersed in deminaralized water. Corneas were isolated by sonicating dissected eyes for several minutes at 47 kHz in a water bath. No significant differences were found between diameters and radii of curvature of the outer surface of the facets before (i.e. in the intact eye) and after isolation. The diameter of the facet lens was taken as the diameter of the largest inscribed circle.

Interference microscopy

Small sections of corneas of the DRA and the DA were selected for Jamin-Lebedeff interference microscopy. These sections were immersed, in sequence, in demineralized water and in immersion oil in a special, closed chamber. The optical paths, G_w and G_o (in water and oil, respectively), were determined with quartz or calcite compensators, yielding the value of the axial refractive index of the cornea n_c, and the geometrical thickness, t. Since $G_w = t(n_c - n_w)$ and $G_o = t(n_o - n_c)$, with n_w and n_o the refractive index of water and oil, respectively, it follows that $n_c = (G_o n_w + G_w n_o)/(G_w + G_o)$. All measurements were performed with 546 nm light (Schott DAL interference filter); $n_w = 1.334$ and $n_o = 1.513$. (For further details, see Stavenga et al. 1990).

Measurement of focal distance

The focusing properties of the facet lenses were assessed by two methods. The first one, was direct measuring of the distance between the inner corneal surface and the backfocal plane. The eye tissue was removed from a freshly cut eyecup by a thin stripe of filter paper. The eyecup was then rinsed by a Ringer solution and the cleaned cornea was placed on a coverslip with its distal side exposed to air. Finally, the preparation was sealed in a moist chamber, as described by Nilsson et al. (1987) and put at the stage of the Olympus BH-2 photomicroscope. Then the lateral eye lenses facing the condenser lens of the photomicroscope were observed. The inner corneal surface was identified by a small number of brown pigment granules fixed to this surface after rinsing with a Ringer solution. The position of the backfocal plane was found by a sharp image of the field diaphragm of the microscope with a specially mounted needle. The accuracy of reading was 1 μm. The DRA facets were examined in the same manner.

The second method, diffractional, allowed to measure the distance between the nodal point of the lens and the backfocal plane by imaging a point light source by the facet lenses in isolated corneas

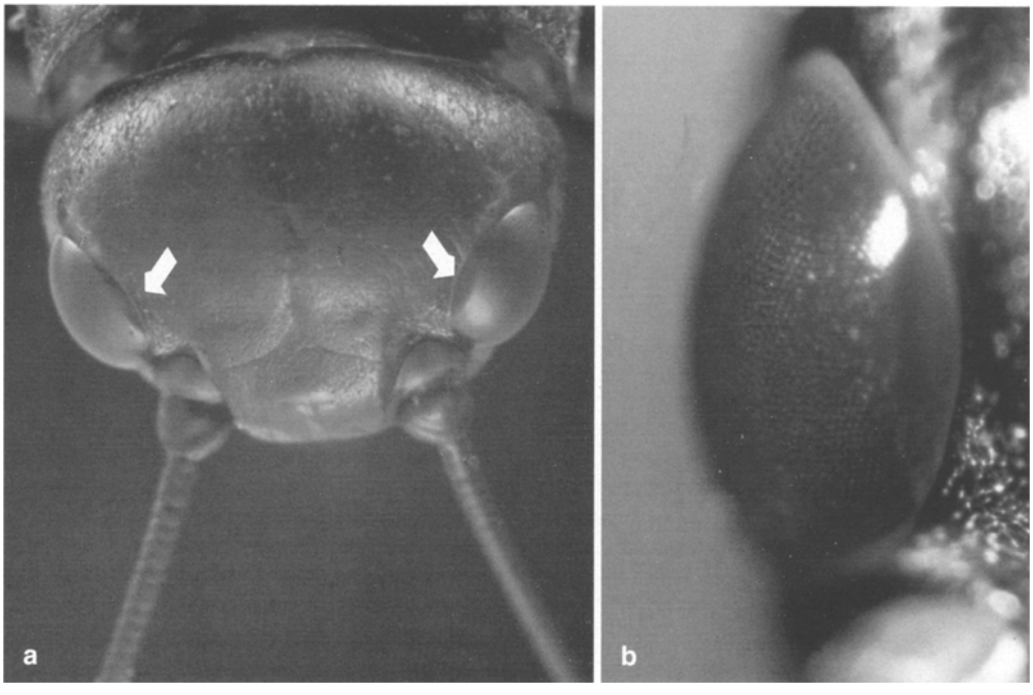

Fig. 1 **a** Head of the cricket *Gryllus bimaculatus* (magnification 14 ×). The narrow dorsal rim areas (DRA) of both eyes, visible as narrow ellipses, are indicated by *arrows*. **b** Dorsal view of the right eye showing the smooth corneal surface of the DRA, together with the adjacent dorso-lateral area, where *dots* indicate corneal reflections from the convex lens surface (magnification 39 ×)

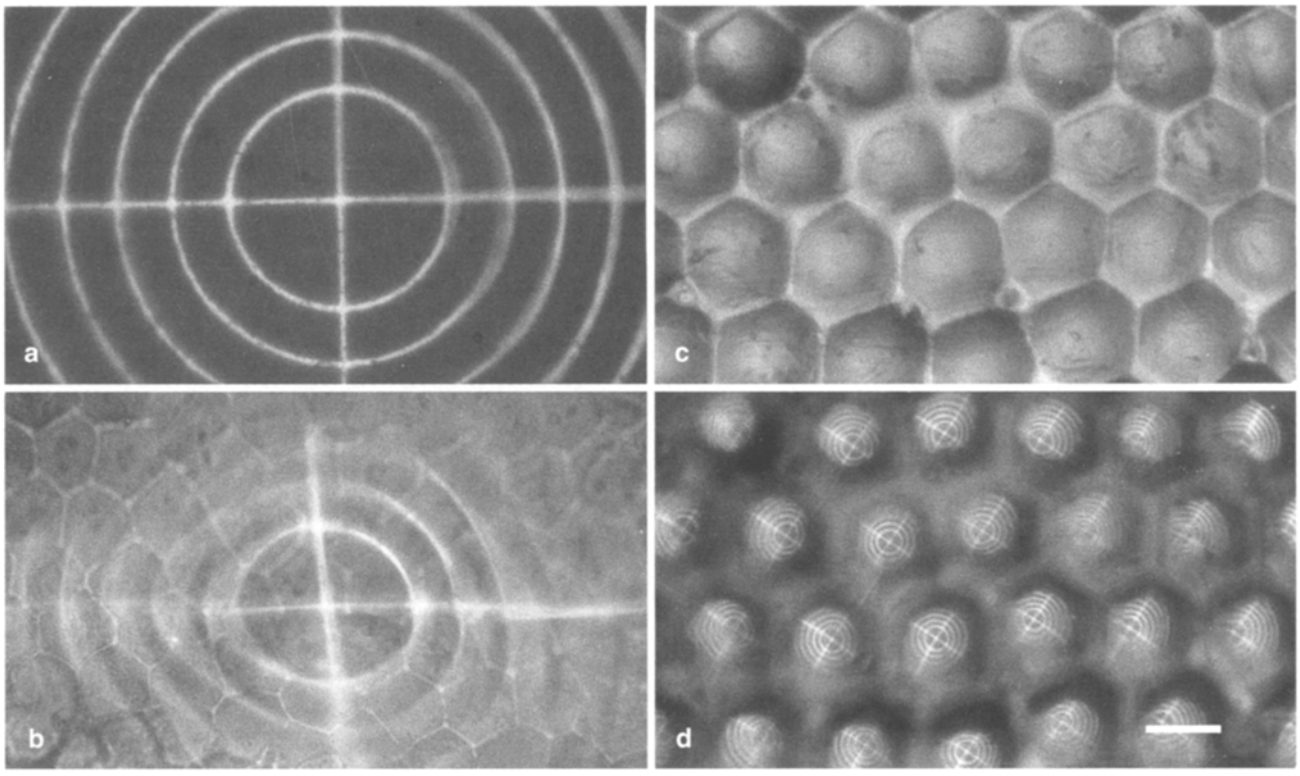

Fig. 2 **a** Image of the annulus pattern used in microreflectometry reflected by a flat mirror. **b** The pattern imaged by the DRA cornea. **c** Epi-illuminated outer surface of the dorso-lateral area cornea. **d** The image of the pattern reflected from the same array of the dorsal facets. *Scale bar* is 20 μm for **a** and **b**, and 35 μm for **c** and **d**

(see Stavenga and van Hateren 1991). A carefully excised piece of isolated cornea was waxed in a hole, drilled in a holder, and mounted under a water immersion objective (Zeiss 40 W, NA 0.55). A small pinhole inserted in the plane of the aperture diaphragm of the condenser was illuminated by a 150 W Xenon lamp via the 546 nm interference filter. The resulting diffraction patterns behind the facet lenses were photographed with the Zeiss photomicroscope, in steps of 10 μm beginning at the cornea surface.

The negatives were analyzed with a microdensitometer (MKIII, Joyce and Loeble, England) by scanning along two perpendicular axes through the center and averaging the resulting data. The focal distance of the facet lens, f, was determined from the radius of the first ring of the Airy-like diffraction pattern, using $f = D\rho_A/(1.22\lambda)$, with D the facet lens diameter, ρ_A the radius of the first Airy ring, and λ the wavelength of the test light (for further details, see Stavenga and van Hateren 1991).

Light microscopy

To perform anatomical measurements, freshly dissected eyes of the crickets from the same breeding stock were fixed for 2 h at 4°C in 2.5% glutaraldehyde in 0.1 *M* phosphate buffer (pH 7.4), and then postfixed for 4 h in 1% OsO_4 at room temperature. Following dehydration tissue was embedded in Epon 812. Sections of 1 μm thickness were prepared on the LKB ultratome, stained with Methylene Blue and examined in the Olympus BH-2 photomicroscope. In several cases isolated pieces of cornea were stained with fluorescein and photographed from their sides to investigate the shape of corneal lenses.

Results

Packing and shape of the facet lenses

In the dorso-lateral area (DA) of the cricket eye, the facets are packed in a regular, hexagonal or somewhat orthogonal array (Fig. 2c). In the dorsal rim area (DRA) the lattice can be quite irregular (Fig. 3b), but most of the facets are also packed in a hexagonal array (Figs. 4d and 5b). In cross-section, the facets in the DRA appear to be half the size of those in the DA. According to individual lens measurements, the facet lens diameter in the DRA is 15 ± 2 μm ($n = 14$), while in the DA the value is 34 ± 2 μm ($n = 13$). When measured as the average from many lenses in a line over the cornea, the DRA lens diameter was 15–16 μm and the lens diameter in the DA was 33–35 μm (more than hundred lenses from eight eyes of four animals were measured). These values are in the same range as given by Burghause (1979) for the DA. Notwithstanding their different size, the dioptrics of the facet lenses in the DRA and DA appears to be qualitatively similar as it is described below. The axial lens thickness of the DA facets was calculated from the interference microscopy data to be 56 ± 1 μm. At the transition line where the corneal surface is bent to form a practically flat DRA surface, the thickness of the corneal lenses is minimal, i.e. only about 30 μm. Then it quickly grows up to 77 ± 3 μm forming DRA corneal lenses.

In preparations stained with fluorescein or methylene blue, the cornea of the eye was usually seen to be made of two layers. The outer layer forms biconvex lenslets and the inner layer forms concave-convex lenses. At the transitional zone, where the DA bends to become the DRA, the inner layer gradually gets down (over the width of several facets), and the outer layer is growing in thickness so that the DRA lenses are seen to be formed exclusively from the material of the outer layer. We made no attempts to investigate the chemical and optical nature of these layers.

Radius of curvature of the facet lenses

The radius of curvature of the facet lens of insect ommatidia often is an important determinant of the power of the dioptrical apparatus (Stavenga et al. 1990). We therefore determined the radius of curvature of both the outer and the inner surface by microreflectometry (see Materials and methods).

The curvature measurements, performed on intact as well as isolated cornea of the cricket *Gryllus bimaculatus*, support earlier findings of an almost flat cornea in the DRA (Burghause 1979; Stavenga 1989). We were unable to determine the curvature of the DRA facet lenses by microreflectometry, because the image of the annulus pattern produced by the individual facets were badly distorted and could hardly be discerned (Fig. 2b). Indeed, the facet lenses in the DRA are nearly flat and thus the whole cornea behaves like a slightly curved mirror (Fig. 2b). On the other hand, the inner surface of the facet lenses in the DRA appears to be rather strongly curved. The reflectance of the inner surface is low, probably because the refractive index is close to that of water. Therefore we could measure the radius of curvature of only a few facets, yielding $R_i = 12 \pm 2$ μm ($n = 6$) in the DRA. In the DA, the radius of curvature of the outer surface of the facet lenses was determined at $R_0 = 172 \pm 8$ μm ($n = 13$), while for the inner surface $R_i = 27 \pm 4$ μm ($n = 15$). The general feature hence is that the outer surface is much less curved than the inner one.

Refractive index

The axial optical path of the facet lenses in both parts of the eye was determined by Jamin-Lebedeff interference microscopy on pieces of isolated cornea immersed in deionized water or immersion oil (Fig. 3). The average axial refractive index of the facet lenses in the DRA was determined at $n_c = 1.496 \pm 0.008$ ($n = 42$) and in the DA at $n_c = 1.469 \pm 0.004$ ($n = 39$). The calculated geometrical thickness in the DRA was 77 ± 3 μm ($n = 42$) and in the DA was 56 ± 1 μm ($n = 39$).

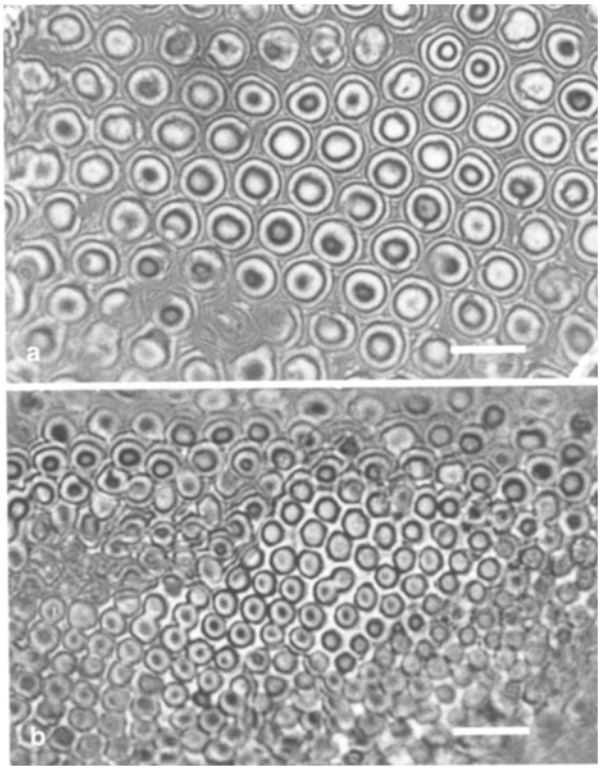

Fig. 3a, b Interference micrographs showing apparent rotational symmetry of the optical path difference of the facet lenses in both parts of the cornea of *G. bimaculatus*. **a** Dorso-lateral area. **b** DRA. *Scale bar* is 55 μm

Focal distance

The direct measurement of position of the backfocal plane (6 eyes from three males, Table 1) shows close similarity to the values obtained from the diffraction experiments (Table 2). The focal distances in the DA are clearly dependent on the individual animal (Table 1). Because all the five DRAs measured gave similar focal distances we averaged this value as 40 ± 8 μm ($n = 84$). The optical quality of the corneal lenses (deduced from the sharpness of the image) over the DRA, which is formed in its widest part by 13–15 rows of ommatidia, is poor in rows 1–5 counting from the head capsule, but it is practically perfect over row 6–15.

Table 1 Backfocal plane positions of the cricket facet lenses

Animal No.	Eye preparation	Focal distance, μm	
		DRA	DA
1, male	right	not measured	95 ± 7 (8)
	left	39 ± 9 (15)	82 ± 9 (7)
2, male	right	39 ± 9 (20)	75 ± 7 (10)
	left	42 ± 8 (20)	80 ± 8 (10)
3, male	right	39 ± 5 (15)	61 ± 6 (12)
	left	40 ± 7 (14)	58 ± 6 (15)
Averaged total		40 ± 8 (84)	

Table 2 Optical characteristics of the cricket facet lenses

	Dorsal rim area (DRA) mean ± SD (number of facets)	Dorsal area (DA)
Diameter (μm)	15 ± 2 (14)	34 ± 2 (13)
Radius of curvature R_0 (μm)	not measured	172 ± 8 (13)
Radius of curvature R_i (μm)	12 ± 2 (6)[a]	27 ± 4 (15)
Axial refractive index	1.496 ± 0.008 (42)	1.469 ± 0.004 (39)
Geometrical thickness (μm)	77 ± 3 (42)	56 ± 1 (39)
Focal distance (μm) – Airy pattern	40 ± 5 (10)	81 ± 8 (11)
Effective cone length (μm)	58 ± 3 (9)	71 ± 5 (16)

All the data obtained from several animals of both sexes
[a] Successful measurements from the cornea of a single animal

Diffraction provides an alternative route for estimating the focal distance and the performance of the lens. From photographs like those in Fig. 4 we could obtain the optical density profiles of the diffraction patterns at different distances behind the surface of the cornea. The focal distance then was determined from measurements of the radius of the first dark ring of the Airy pattern (see Materials and methods). The resulting focal distances for the DRA facet lenses were 40 ± 5 μm ($n = 10$) and for the DA facet lenses were 81 ± 8 μm ($n = 11$) (Table 2), in good correspondence with the values obtained from direct imaging.

To validate our measurements of the focal distances we measured the effective length of crystalline cone in both DRA and DA from histological sections. It is known that in the cricket compound eye the crystalline cone is immersed in the rhabdom like a wedge. We assume that the distance between the inner surface of the facet lens and the distal end of the rhabdom is the effective length in terms of the optics. In the DRA the effective cone length thus defined was 58 ± 3 μm ($n = 9$), while in the DA it was 71 ± 5 μm ($n = 16$) (Table 2).

Discussion

The dorsal rim area (DRA) of the compound eye of many insect species is uniquely specialized for sensing polarized light (Wehner and Strasser 1985; Brunner and Labhart 1987; Labhart 1986; von Philipsborn and Labhart 1990; Labhart et al. 1992). Unlike in other species, the DRA of crickets completely lacks screening pigments, while the photoreceptors in that area exhibit an amazingly high polarization sensitivity (Labhart et al. 1984; Gribakin and Ukhanov 1993b). In the cricket DRA photoreceptors, the amount of guided light was reported to be only 20% (Nilsson et al. 1987), implying that optical coupling plays a minor role in enhancement of the polarization sensitivity.

In our search for a specific light-scattering or linear polarizer we have first analyzed the dioptrics of the corneal facet lenses in the cricket DRA, and dorso-lateral area (DA). We found that the facet lenses of the DRA behave quite normally, i.e. similar to those in the rest of the eye, and exhibit no optical anomalies. Corneal facet lenses from both parts of the cricket compound eye showed no properties of a linear polarizer, but have well pronounced birefringence, especially in the dorso-lateral area (Fig. 5). However, this effect can hardly contribute to light polarization and therefore has no importance in enhancing the polarization sensitivity.

In the cricket compound eye most of the geometrical parameters of the facets in the DRA were half of those in the DA (Tables 1, 2). Both direct measurements of the backfocal plane position and analysis of the diffraction pattern gave similar results in all the eye regions, and this means that the nodal points of the corneal lenses are located close to the inner corneal surface. The fact that the SD of the focal distance of the DRA facets appeared to be two times higher as compared to the DA lenses indicates the larger variability in this population of lenses. In the DRA we found the effective cone length of 58 ± 3 μm. Thus, the DRA facet lenses appear to be slightly underfocused. The effective cone length in the DA, 71 ± 5 μm in our preparations (cf. about 66 μm in *Gryllus campestris*, Fig. 1 in Nilsson et al. 1987) is in good agreement with the focal distance of the facet lens measured in the DA. The focal distance varies between 60–90 μm, presumably determined by the size of the animal. These findings are in line with the data that the ommatidial optical design in the main body of the compound eye is aimed to yield maximal spatial resolution. In the DRA fine optical tune is not a goal. Several manifestations of such an optical mismatch are the disturbed light-guide properties of the rhabdoms in *Gryllus campestris* (Nilsson et al. 1987), missing crystalline cones in *Cycloptiloides canariensis* (Egelhaaf and Dambach 1983) and the completely absent pigmentation of the DRA in *Gryllus bimaculatus* (Burghause 1979).

Comparison of the optical parameters of the compound eyes of known white-eyed mutants with those of the DRA could give us valuable information concerning light-scattering. Recently we have measured that up to 70% of the effective light in the non-pigmented eyes

of blowfly *chalky* mutants is due to light-scattering, even when using a point light-source (Gribakin and Ukhanov 1993a). Despite this substantial off-axis illumination, the angular sensitivity profile of the honeybee *snow* and blowfly *chalky* photoreceptors remains to be distinct, displaying "a hat with brims", with the acceptance angle within about 5° (Streck 1972; Gribakin 1988, honeybee *snow*; our own observations in the blowfly mutant *chalky*). This fact indicates that, in the white eye, the corneal lenses are still capable of

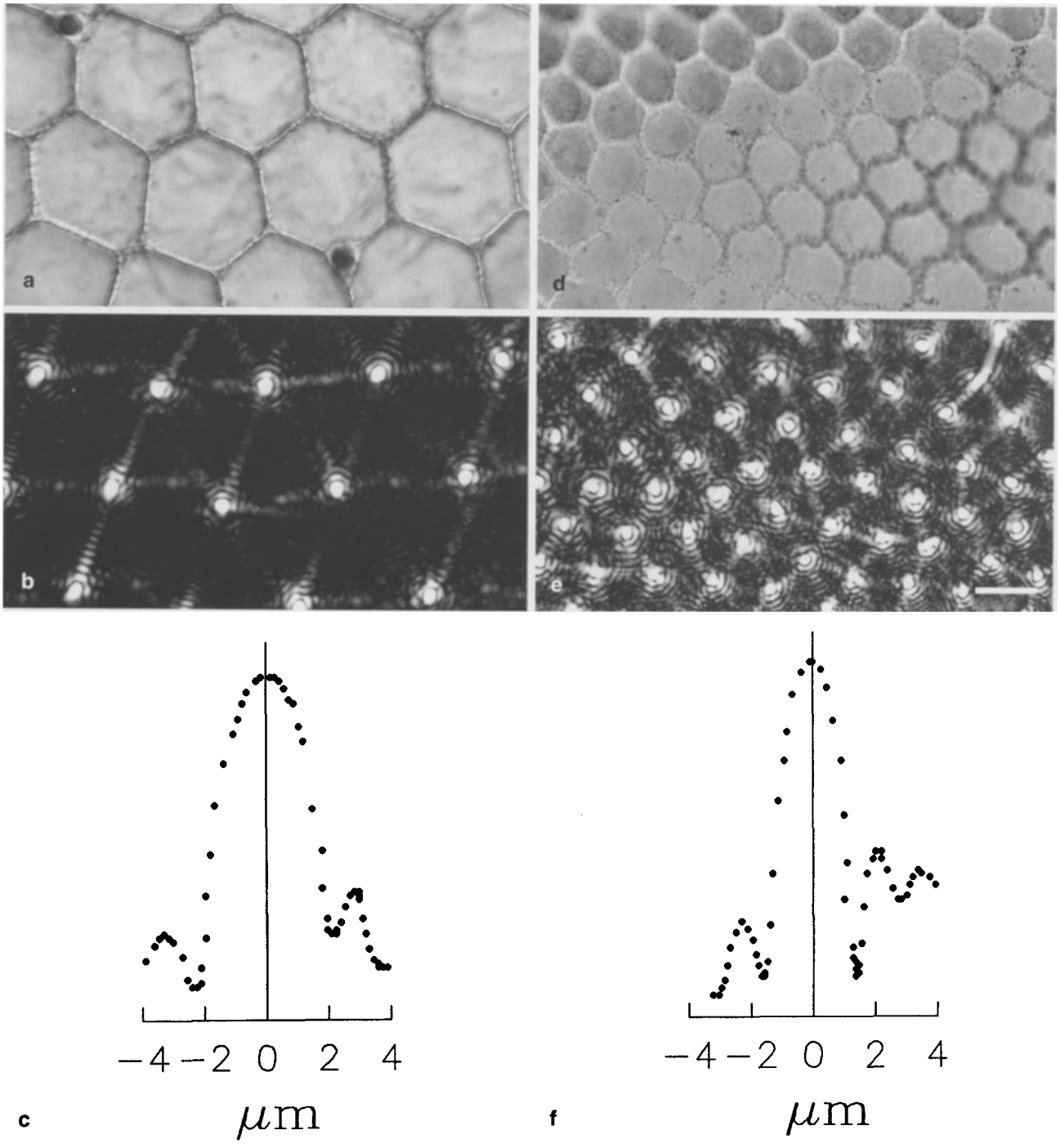

Fig. 4a–f Diffraction patterns, due to a point light source, focused by the facet lenses were analyzed densitometrically. **a** The array of the dorsal facet lenses used for further analysis. **b** Diffraction pattern viewed at the focal plane behind the lens. **c** Axial profile of the digitized optical density distribution of the Airy-like pattern resulting from an individual facet lens and viewed at the same distance as in **b**. **d** Analogous portion of the DRA cornea. **e** The pattern viewed at the focal plane position behind the lens. **f** Axial profile at the same distance as in **e**. *Scale bar* is 20 μm for all subfigures

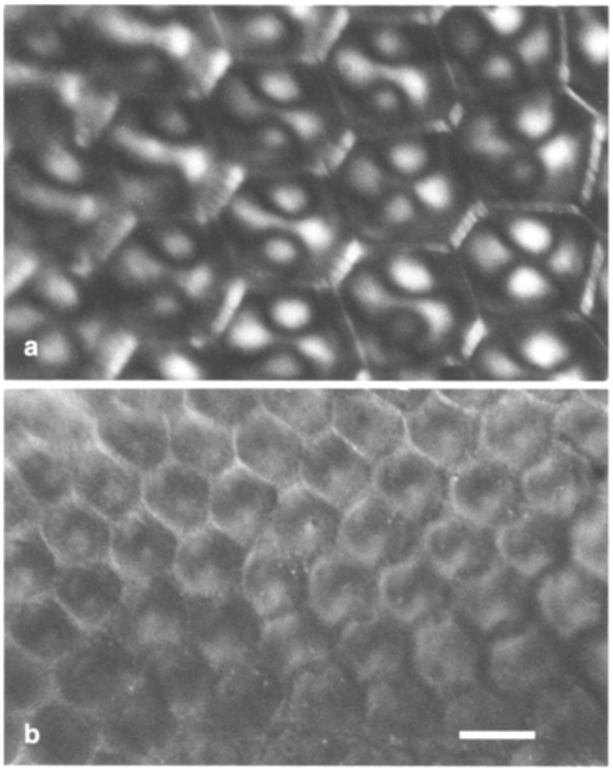

Fig. 5 **a** Dorsal cornea observed in cross-polarized illumination. **b** The same illumination for the DRA cornea. *Scale bar* is 25 μm for both figures

focusing light onto the waveguiding rhabdoms. Clearly, the absence of screening pigments alone is insufficient for explaining the dome-like angular sensitivity curves of the DRA photoreceptors found in crickets (Labhart et al. 1984; Zufall et al. 1989; own measurements). On the other hand, in hymenopterans, with their normally pigmented DRAs, visible as "grey zones", hat-like angular sensitivity functions (Labhart 1980) can be well explained by strong light scattering produced by special corneal structures (Meyer and Labhart 1981).

In the present study we have shown that the corneal facet lenses of the DRA of crickets are neither linear polarizers nor light scattering elements. In this case, wide and smooth, dome-like visual ffields of the cricket DRA photoreceptors might be accounted for by the properties of the ocular medium itself which, apart from the strong light scattering inherent to the non-pigmented "white eye", likely minimizes the light-guide properties of the DRA rhabdoms (cf. Nilsson et al. 1987). Another tentative source of the stray light could be an underfocusing of incident light by the facet lenses. This must be the case in the DRA of the cricket *Cycloptiloides canariensis* (Egelhaaf and Dambach 1983). Underfocusing of the incident light by the facet lenses in addition to depigmentation means that the off-axis stray light must be dominant in the DRA and photoreceptors could use it as a major source for sensing of the light polarization.

Another important question is the directionality of the polarization sensitivity. In the cricket DRA, rhabdoms of the photoreceptors are arranged in a fan-like array (Burghause 1979; Labhart et al. 1984). This is a direct indication for different E-vector sensitivities of neighboring photoreceptors. Very similar to the cricket DRA, photoreceptors are organized in so-called POL-areas in the compound eyes of several other insect species: hymenopterans (Schinz 1975; Wehner 1994), lepidopterans (Meinecke 1981; Kolb 1986) and dipterans (Wunderer and Smola 1982). Despite the fact that the cricket DRA is flooded with stray light that minimizes light-guiding of the rhabdom, a fan-like organization of the rhabdoms and fine alignment of dichroic microvilli within the rhabdoms will determine the E-vector sensitivity.

We conclude that the hypothesized DRA scattering polarizer of the cricket *Gryllus bimaculatus* is not located at the level of the corneal facet lenses. Further efforts will elucidate whether scattering and defocusing of light in the interommatidial matrix could enhance polarization sensitivity of the DRA photoreceptors in the cricket eye.

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